ON THE ORIGIN OF POLAR CONJUGATION IN THE ANGIOSPERMS.

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Various attempts have been made to explain the probable origin of the remarkable structures and activities present in the embryosac of the Angiosperms. These attempts, however, resulted in mere hypotheses with few or no known facts in their favor to recommend them for serious consideration. With the recent great advance in our knowledge of the female gametophyte of the Gymnosperms, due to the thorough work of a number of zealous observers, has come the opportunity for a reconsideration of the problem in the light of the new discoveries. Porsch[1] has done this in a very interesting and convincing paper in which he presents very strong evidence for his views.

He holds that the two synergids of the Angiosperms are neck canal cells homologous with the neck canal cells of the Gymnosperm archegonium; that the oospheres of Gymnosperms and Angiosperms are homologous cells: and that the upper polar, which is a sister cell of the oosphere, as determined by various observers for different plants and very definitely by the writer for Erythronium,[2] is the homologne of the ventral canal cell of the Gymnosperm archegonium. He holds further that the

1 PORSCH, OTTO. Versuch einer phylogenetischen Erklarung des Embryosackes und der doppelten Befruchtung der Angiospermen. Verlag von Gustav Fischer in Jena. 1907.

2 SCHAFNER, JOHN H. A contribution to the Life History and Cytology of Erythronium. Bot. Gaz. **31** : 369–387. 1901.

lower end of the Angiosperm embryosac is the morphological equivalent of the upper, the lower polar being thus also homologous to a ventral canal cell. In other words, the typical embryosac or female gametophyte of the Angiosperms, with its symmetrical arrangement of four cells at opposite poles, represents two archegonia, the vegetative cells having disappeared.

There is much in favor of this theory from the standpoint of the writer. In 1896, in my paper on Alisma plantago,[3] I made the statement that "Especially in regard to the real meaning of the conjugation of the polar nuclei, and what is represented by the antipodal cells, does there still seem to be much obscurity." But my study of the Angiosperm embryosac gave no light on these two important questions except that I observed the following facts: "The cells in the antipodal region simulate the arrangement in the egg-apparatus. There are two small nuclei lying at the base; and beyond them is the third antipodal nucleus." "It would by its peculiar appearance suggest that it may be *the homologue of the oosphere.*" (Italics not in the original.)

Chamberlain[4] had, in 1895, figured and described what he felt positive was a veritable oosphere in the antipodal region of Aster. It would appear that the extensive antipodal region of Aster still has the ability to develop a structure very similar in appearance to the micropylar egg apparatus. Chamberlain, however, did not take advantage of his remarkable discovery to assert the similar nature of the two ends of the sac, being probably hindered from doing so by a too strict adherence to the prevailing hypothesis that the antipodal region represents the vegetative thallus of the Angiosperm female gametophyte.

If Porsch's view of the homologies is correct, it becomes evident that we have, as he ably shows, an easy explanation of the origin and nature of the triple fusion process, or what has improperly, to my mind, been called double fertilization, which appears to be so common in the Angiosperm sac.

I wish to add an explanation of certain peculiarities not specially touched upon by Porsch. In my paper on Sagittaria latifolia[5] I made the following observations: " approaching each other the upper larger polar nucleus travels much farther than the lower one, so that the place of contact is usually in the lower part of the embryo sac, and the fusion takes place here without any apparent shifting of the nuclei, *the fusion being usually complete before the entrance of the pollen tube into the sac.*"

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3 Schaffner, John H. The Embryosac of Alisma Plantago. Bot. Gaz. **21** : 123–132.

4 Chamberlain, Chas. J. The embryo-sac of Aster Novae-Angliae. Bot. Gaz. **20** : 205–212.

5 Schaffner, John H. Contribution to the Life History of Sagitaria variabilis. Bot. Gaz. **23** : 252–273, 1897.

(Italics not in the original.) The pollentube is so remarkably distinct in Sagittaria and produces such marked changes that I am certain I could not have overlooked it in the stages where polar conjugation takes place, especially since the study of the pollentube was one of the main objects of this investigation.

Thus it is certain that in some plants the polar nuclei have learned to conjugate without the influence of the second sperm nucleus or even the pollentube. The question now arises as to how the polars acquired this remarkable ability if they do not represent opposite sexes. For it seems excluded that one could think of the Angiosperm female gametophyte as being a direct descendant of an hermaphrodite thallus, the polar nuclei being descendants from male and female gametes. It is altogether probable that the Angiosperms passed through the Heterosporous Pteridophyte stage before becoming seed plants. Porsch's view, therefore, seems the correct one, that the triple conjugation results from the essentially female character of the polars. If therefore a conjugation takes place without the presence of the second sperm, this must be looked upon as a special sort of parthenogenetic development. All polar conjugations, accordnig to this view, had their origin in the original conjugation of one or both polars with the second sperm, typically in the second way through triple fusion.

Now the question arises as to whether there is a triple fusion in Sagittaria and other such cases. Does the second sperm come down later and fuse with the polars acquired the property or function of conjugating with each other through their common attraction to the second sperm with the first upper endosperm nucleus after the partition wall is formed at the end of the division of the definitive nuclues? This division takes place about the same time as the first division of the oospore, and such a possibility is suggested by the following facts: The second sperm seems to remain in the tube for some time after the first one escapes to unite with the egg; the upper endosperm nucleus, immediately after the division of the definitive nucleus, begins to travel upwards; the lower endosprem nucleus presents a remarkably different development from the upper one. But no weight is to be attached to the suggestion until further investigations are made.

True endosperm, as has been suggested by several investigators, may be present even in Gymnosperm archegonia. A true endosperm might originate from the division of a ventral canal cell without conjugation of the second sperm with the ventral canal cell. In Angiosperms an endosperm might result from the conjugation of either polar nucleus with the second sperm; from the conjugation of both polars with the second sperm, which seems to be the usual mode; or through partial

parthenogenesis from a definitive cell in the formation of which the two polars alone are concerned; or even possibly from a single polar cell. The lack of fusion of the polars, if such condition exists, may represent either a primitive condition or a more recent, parthenogenetic condition. Theoretically, therefore, it is possible to have an "x" endosperm generation of two different origins, a "2x" endosperm generation of two types differing in constitutional structure, and a "3x" endosperm generation, but none of these could properly be called an embryo.

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